

# The Structure and Function of Neogastropod Reproductive Systems: with Special Reference to *Columbella fuscata* Sowerby, 1832

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(1 Plate; 10 Text figures)

## INTRODUCTION

PREVIOUS STUDIES have indicated that among the Neogastropods there is a similarity in the organization of reproductive systems. This has been most clearly shown in studies of the families Muricidae, Buccinidae, and Nassariidae (FRETTER, 1941; JOHANSSON, 1942, 1947; FRETTER & GRAHAM, 1962; PURCHON, 1968). In addition, there are descriptions of the reproductive systems of a few species of other Neogastropods from the families Olividae, Terebradae, Fasciolaridae, Columbelloidae, and the Turridae (MARCUS & MARCUS, 1959a, 1960, 1962a, 1962b; ROBINSON, 1960; SMITH, 1967). The Panamic region, including the Gulf of California, is enriched with a vast assemblage of gastropods including many endemic species. To date very little work has been done on these species. It is, therefore, valuable to study the function of and the phylogenetic relationships between reproductive systems of a few Gulf species and compare them with those of species in other regions of the world.

The species examined in depth are *Acanthina angelica* I. Oldroyd, 1918 and *Columbella fuscata* Sowerby, 1832. According to KEEN (1971), *A. angelica* is endemic to the Gulf of California. In contrast, *C. fuscata* occurs throughout the Gulf and south to Peru. In addition, 8 other species from the Gulf of California and 15 species from other regions of the world were examined briefly for comparative purposes (Table 1).

Table 1

## Additional Species and Their General Localities

Species	Locality
I. Muricidae	
A. <i>Thais haemastoma</i> (Linnaeus, 1767)	São Paulo, Brazil
B. <i>Thais emarginata</i> (Deshayes, 1835)	California, U.S.A.
C. <i>Thais canaliculata</i> (Dulcos, 1832)	California, U.S.A.
D. <i>Ocenebra japonica</i> (Dunker, 1860)	California, U.S.A.
E. <i>Urosalpinx cinerea</i> (Say, 1822)	California, U.S.A.
F. <i>Acanthina spirata</i> (Blainville, 1832)	California, U.S.A.
G. <i>Ceratosoma foliatum</i> (Gmelin, 1791)	California, U.S.A.
H. <i>Drupa nodulosa</i> (Adams, 1862)	São Paulo, Brazil
I. <i>Trophon truncatus</i> (Strom, 1768)	Millport, Scotland
J. <i>Trophon barvicensis</i> (Johnston, 1825)	Millport, Scotland
II. Buccinidae	
A. <i>Neptunea antiqua</i> (Linnaeus, 1758)	Millport, Scotland
B. <i>Colus gracilis</i> (da Costa, 1778)	Millport, Scotland
C. <i>Pisania janerensis</i> (Philippi, 1848)	São Paulo, Brazil
D. <i>Cantharus d'orbigny</i> (Link, 1807)	São Paulo, Brazil
III. Columbelloidae	
A. <i>Columbella strombiformes</i> (Lamarck, 1822)	Sonora, Mexico
B. <i>Anachis nigrofusca</i> (Carpenter)	Sonora, Mexico
C. <i>Anachis coronata</i> (Sowerby, 1832)	Sonora, Mexico
D. <i>Anachis sanfelipensis</i> (Lowe, 1935)	Sonora, Mexico
E. <i>Anachis varia</i> (Sowerby, 1832)	Sonora, Mexico
F. <i>Anachis hilli</i> (Pilsbry and Lowe, 1932)	Sonora, Mexico
G. <i>Parametaria duponti</i> (Kiener, 1849-1850)	Sonora, Mexico
H. <i>Mitrella guttata</i> (Sowerby, 1832)	Sonora, Mexico
IV. Nassariidae	
A. <i>Nassarius incrassatus</i> (Strom, 1768)	Millport, Scotland

## METHODS AND MATERIALS

Monthly samples of specimens were collected over a period of 2 years from Puerto Peñasco, Sonora, Mexico. There were 10 individuals of each species in each sample. Both *Acanthina angelica* and *Columbella fuscata* occur in the rocky intertidal zone at Station Beach, which is located one mile south of Puerto Peñasco.

The snails were then transported alive in styrofoam containers to the University of Arizona where they were maintained in plastic aquaria for laboratory investigations.

General descriptions of the genitalia were made after careful dissections of both preserved and living material, while stained sections of the reproductive tract were examined in order to elucidate the components and cellular details. The soft parts were removed from their shell with the aid of a vise. They were then relaxed in propylene phenoxylol (OWEN, 1955) and fixed in Bouin's fluid. Through the use of standard histological techniques, the animals were infiltrated with 52.5°C and 56.5°C paraffin and sectioned at 19  $\mu$ m. The sections were stained with Kornhouser's Hemalum and Eosin B. Alcian Blue and Mallory's Trichrome were used for identifying glandular parts of the reproductive system. Ciliary current were observed by using suspended carmine particles in sea water.

A detailed analysis of the functional aspects of reproduction was studied for *Columbella fuscata* only. The snails were periodically observed, and during times of reproductive activity, both males and females were preserved before, during, and after copulation. They were later dissected and sectioned to determine sperm and egg movements, site of fertilization, egg capsule formation, and the mechanism of sperm ingestion.

Juveniles of *Acanthina angelica* and *Columbella fuscata* were also collected to study the development of the genital systems. Their shell length was determined by measuring with vernier calipers the distance from the top of the spire to the tip of the siphonal canal.

## RESULTS

Because this study concentrates on two species of Neogastropods, detailed descriptions of their genital systems are treated first. The reproductive morphology of the remaining 23 species is discussed secondarily with a brief account of the major structural differences and similarities.

### The Male Duct

The male ducts of both species are illustrated in Figures 1a, 1b.

### *Acanthina angelica*

Posteriorly, both the testis (te) and the digestive diverticula share the visceral mass. From the testis the straight vas deferens (vd) leads anteriorly, ventral to the intestine and passes dorsal to the pericardial cavity. Here it joins the prostate gland (pg) in the right posterior region of the mantle cavity. Anteriorly, the large curved prostate gland runs beneath the hypobranchial gland until it connects with the anterior vas deferens. At this point the vas deferens lies embedded in the body wall and continues anteriorly until it joins the penis (pn), which is situated just posterior to the right cephalic tentacle. This system is similar to those of *Nucella lapillus* (Linnaeus, 1758) and *Ocenebra erinacea* (Linnaeus, 1758) described by FRETTER (1941), except for the posterior region of the vas deferens which is coiled.

Histologically the entire posterior vas deferens is thin-walled and surrounded by a thin layer of connective tissue. The lumen is lined with cuboidal ciliated epithelium with round, centrally located nuclei. There is no seminal vesicle in this species, and at no time even during the breeding season was sperm observed in this duct. In *Nucella lapillus*, FRETTER (1941) noted that the coiled vas deferens acts as a seminal vesicle. The entrance to the prostate gland is guarded by a sphincter consisting of circular muscles. The lateral lobes of the prostate bulge due to the development of glandular tissue. The subepithelial gland cells are in the shape of teardrops containing large round nuclei. The cytoplasm contains eosinophilic granules and is highly vacuolated. These gland cells are arranged in clusters where secretions empty into common ducts that lead to the lumen of the prostate. The lumen appears as a dorsoventral slit which is lined with ciliated columnar epithelium. The epithelial cells contain basal oval nuclei and lie on a basement membrane. Interspersed regularly between these epithelial cells are the ducts leading from clusters of subepithelial gland cells. The entire prostate is held together by a thin layer of connective tissue. In addition, the epithelium lining the lumen merges ventrally as a double row of cells, which is the result of fusion of the duct from an originally open groove. The prostate is fused throughout its length except for a posterior region of about 450  $\mu$ m. The unfused region appears as a slit-like aperture which is in communication with the posterior region of the mantle cavity. This differs from *Littorina littorea* (Linnaeus, 1758), *L. obtusata* (Linnaeus, 1758) and *L. rudis* (Maton, 1797) in which the prostate is composed of two glandular lobes and is open throughout its entire length (LINKE, 1933).

Anterior to the prostate the vas deferens is highly muscular and the lumen is lined with ciliated cuboidal epi-



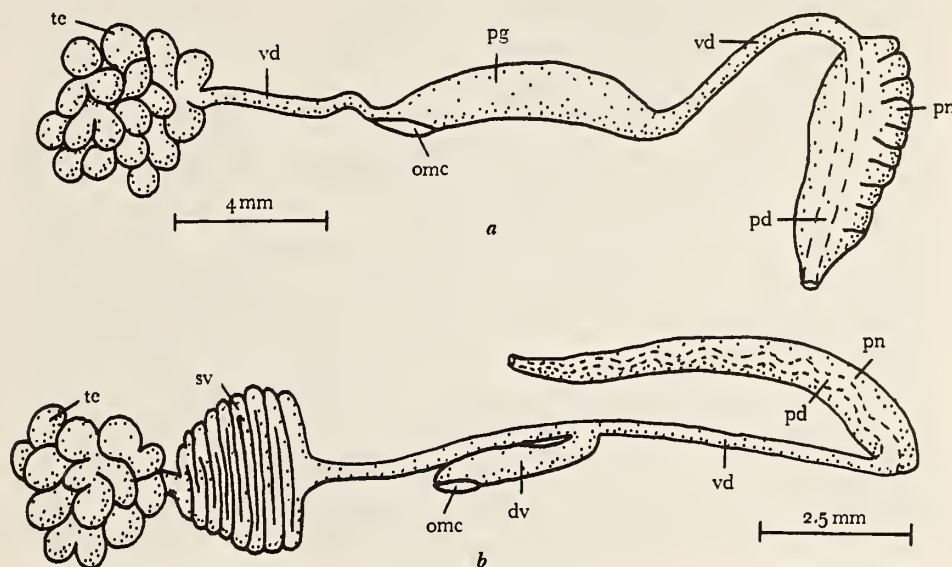


Figure 1

Male Ducts: *a*:—*Acanthina angelica*; *b*:—*Columbella fuscata*  
 dv — diverticulum      omc— opening to the mantle cavity

pd — penial duct      pg — prostate gland      pn — penis  
 sv — seminal vesicle      te — testis      vd — vas deferens

thelium. The line of fusion is evident throughout the anterior vas deferens and the penial duct (pd). The penis is flattened dorsoventrally with the penial duct appearing as a straight canal just dorsal of center. The histology of the penial duct is similar to that of the vas deferens. In cross section the penis appears as a complex network of longitudinal and circular muscle fibers loosely arranged around haemal sinuses. The surface is lined with ciliated columnar epithelium interspersed by ducts leading from subepithelial mucous cells.

#### *Columbella fuscata*

The genital system of *Columbella fuscata* differs markedly from that of *Acanthina angelica* in several respects. The upper vas deferens is highly convoluted and acts as a seminal vesicle (sv). This seminal vesicle is divided into two regions. When examined, the posterior half appears white due to the presence of stored sperm. The anterior region is yellowish brown, and it is in this area that sperm are apparently resorbed. The walls of the seminal vesicle are quite thin and appear rather rigid when filled with sperm. The vesicle is lined with ciliated cuboidal epithelium resting on a basement membrane below which is a thin layer of connective tissue. The epithelial cells con-

tain large round basal nuclei and distal yellowish brown inclusions which may be the products of sperm resorption. Anteriorly, the seminal vesicle straightens out for a short distance until it reaches the posterior region of the mantle cavity, where it becomes the true vas deferens. It passes anteriorly and parallel to the rectum, where in this region it bends upward and runs along the body wall until it joins the base of the penis. There is no prostate gland in *C. fuscata*. A study by MARCUS & MARCUS (1962b) on Brazilian columbellids revealed the absence of a prostate in *Anachis veleda* (Duclos, 1846), *A. brasiliiana* (von Martens, 1897), *A. sparsa* (Reeve, 1859), and *Nitidella dichroa* (Orbigny, 1842). A sphincter is present between the seminal vesicle and vas deferens, which controls entry of sperm into the latter. The epithelial cells lining the vas deferens are not as strongly ciliated as those of the seminal vesicle. However, the vas deferens is extremely muscular and assumes an ejaculatory function. As shown in Figure 1b, the vas deferens ventrally gives rise to a long, thin-walled diverticulum (dv), which passes ventrally and parallel to the duct. A sphincter guards the entrance between the vas deferens and the diverticulum. The posterior region of the diverticulum is open to the mantle cavity by a ventral slit 450  $\mu$ m in length. On several occasions sperm masses (sp) were observed escaping through this opening (Figure

11). The function of this opening will be discussed later. No line of fusion is evident as in the case of *Acanthina angelica*.

The penis, while dorsoventrally flattened, is much longer than that of *Acanthina angelica*. Moreover, it is wide at the base and then tapers to a point. The penial duct is centrally located and appears as a convoluted tube which opens at the tip of the penis. In resting males, the penis is curved back along the right side of the body wall. When the mantle edge is pulled back, one can see that the tip is tucked in a pouch in the posterior mantle wall. This

has been observed in other columbellids (MARCUS & MARCUS, 1962b).

### The Female Duct

Female ducts of both species are presented in Figures 2a, 2b.

#### *Acanthina angelica*

The genital duct of this species is similar to that of *Nucella lapillus* described by FRETTER (1941). The ovary (oa)

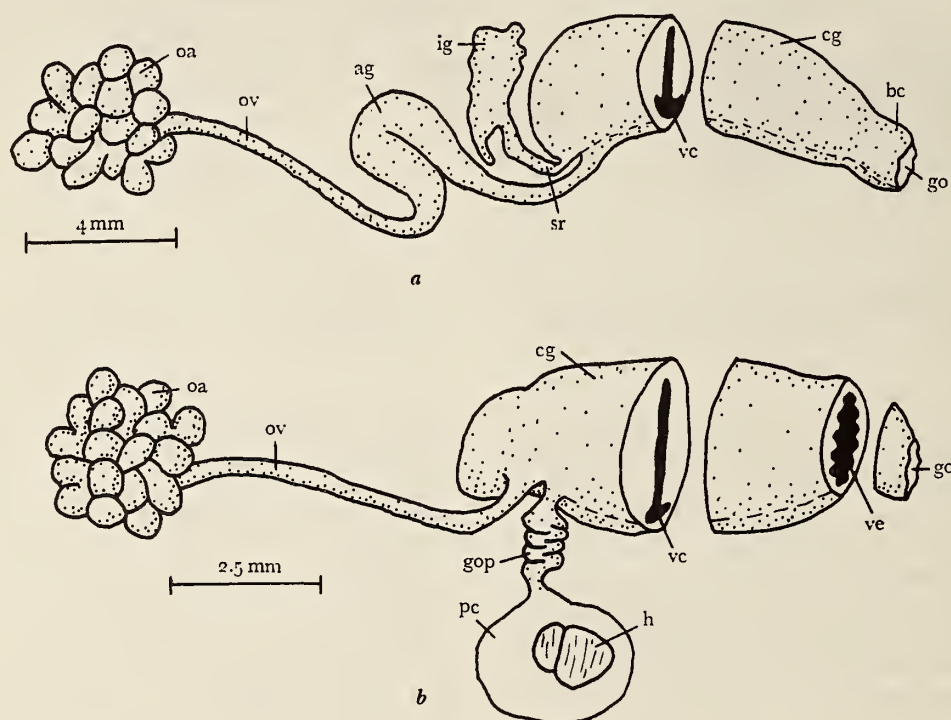


Figure 2

Female Ducts: a: - *Acanthina angelica*; b: - *Columbella fuscata*  
ag - albumin gland bc - bursa copulatrix cg - capsule gland  
go - genital opening gop - gonopericardial duct h - heart

ig - ingesting gland oa - ovary ov - oviduct  
pc - pericardial cavity sr - seminal receptacle  
vc - ventral channel ve - vestibule

### Explanation of Figures 11, 12

Figure 11: Section through the opening to the mantle cavity in a male *Columbella fuscata*: dv - diverticulum; omc - opening into the mantle cavity; sp - sperm escaping through the opening  
Figure 12: Section through the pericardial cavity of *Columbella fuscata*: sp - sperm; h - heart



Figure 11

160  $\mu$ m

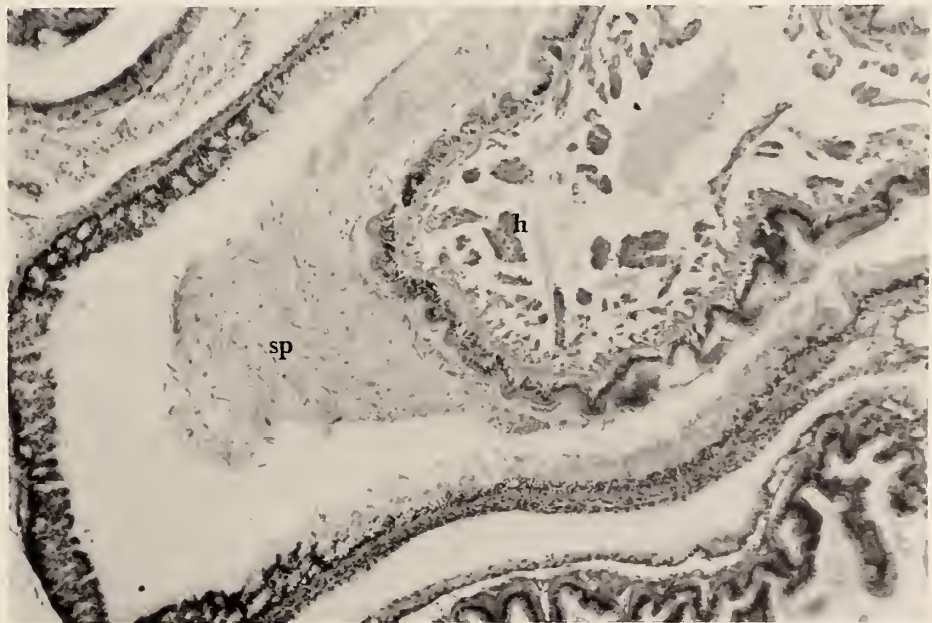


Figure 12

360  $\mu$ m





and the digestive diverticula share the upper whorls of the visceral mass. From the ovary the thin-walled oviduct (ov) leads anteriorly and ventrally along the right side of the viscera. Upon dissection, it appears as a large blood vessel just below the integument. In the region of the kidney it approaches the albumin gland (ag), which doubles back on itself, thereby making a sharp angle with the oviduct. The albumin gland then opens into the capsule gland (cg), which is divided into right and left glandular lobes. These lobes are joined together by dorsal and ventral sutures and covered with a thin layer of connective tissue. Lying between the albumin and capsule glands is a deep brown, highly diverticulated glandular mass, the ingesting gland (ig). A duct from this gland opens into the posterior region of the capsule gland. The capsule gland continues forward and ventral to the anal gland, where it leads to a vestibule. Anterior and ventral to the vestibule is a blind muscular sac, the bursa copulatrix (bc), which receives sperm from the male. The bursa and vestibule join to form the short ciliated vagina that leads to the genital opening (go) proximal to the anus.

The oviduct is thin-walled and lined with a single layer of ciliated cuboidal epithelium resting on a basement membrane. As it approaches the albumin gland, the oviduct becomes heavily laden with circular muscle cells, which act as a sphincter controlling the entrance to the albumin gland.

When the shell is removed from a living specimen, the albumin gland can be seen as a white opaque mass lying dorsal and just posterior to the pericardial cavity. Internally it is ciliated throughout, with the lumen containing transparent secretory droplets. Sections reveal a circular gland with a ciliated dorsoventral lumen. There are two major staining regions in this gland. The right side of the gland is composed chiefly of mucous cells which stain bright blue, while the left half is made up of groups of subepithelial gland cells that stain pink with Eosin B. The latter cells are oval with large round nuclei and have ducts which open into the lumen between the epithelial cells. A short duct connects the albumin gland to the posterior region of the capsule gland. Transverse sections reveal two lobes of equal size with the lumen appearing as a dorsoventral slit. The lumen is ciliated throughout. Running the length of the gland are two longitudinal flaps of tissue, which form the roof of the ventral channel. The left flap is more developed and lies over the right one, thereby possibly closing off the ventral channel and making it a functionally separate duct.

The subepithelial gland cells are teardrop shaped and have a long thin duct which opens into the lumen between the epithelial cells. Anteriorly the capsule gland is com-

posed of mucous cells, which are scattered around the ventral channel and extend throughout both lobes. This configuration continues throughout the anterior one-fourth of the gland, until it is replaced by two other cell types. Cells around the ventral channel stain dark purple with Kornhouser's Hemalum, while the cells in the medial region of the gland stain pink with Eosin B. Mucous cells are limited to the dorsal region. About one-half way through the gland, the purple cells extend into the medial regions, leaving only a thin strip of pink staining cells in this area. Finally, in the posterior quarter, the purple staining cells occupy the ventral and medial regions, while mucous cells are scattered throughout the dorsal region.

The ciliated ventral channel (vc) passes ventrally from the bursa copulatrix, extends posteriorly through the capsule gland and joins the duct to the ingesting gland. This duct is without cilia and functions as a seminal receptacle (sr). Here spermatozoa are neatly aligned, with their heads embedded in the epithelium, and their tails projecting into the lumen. The ingesting gland is a sac composed of many blind tubules, lined with glandular epithelium, which break down and metabolize the sperm (FRETTER, 1941). The bursa copulatrix, which comprises the anterior end of the capsule gland, is covered by a layer of circular muscle cells and lined with ciliated columnar epithelium lying on a basement membrane. This anterior bursa receives sperm deposited by the male.

#### *Columbella fuscata*

The female system of this species is quite different from that of *Acanthina angelica*. The bright yellow ovary lies on the outer surface of the visceral mass and is separated from the digestive gland by a thin layer of connective tissue. The ovary consists of many acini which collectively funnel into the upper end of the oviduct. The individual acinus is lined with various cell types, including epithelial cells, secretory cells, and primordial sex cells. Oogenesis occurs in a developmental gradient from the periphery to the center of the acinus. The mature ovum is attached by a peduncle to a peripheral nurse cell, and pink staining yolk granules and other secretory droplets fill the lumen of the acinus. The long, transparent oviduct runs along the ventral edge of the ovary and passes down the right side of the viscera. Ventral to the kidney it opens into the capsule gland. There is no albumin gland in this species. The entrance to the posterior region of the capsule gland is guarded by a sphincter muscle. The oviduct is thin-walled and lined with cuboidal ciliated epithelium.

In the living animal, the capsule gland is an opaque, creamy white, glandular mass. In reproductively active individuals this gland will attain a thickness of about 2 mm

and a length of 5 mm. It is ciliated throughout, and in cross section the lumen appears as a dorsoventral slit with short diverticula extending into the lobes. The ventral channel, extending the length of the gland, has fewer cilia which,

Table 2

Cell Types in the Capsule Gland of *Columbella fuscata*

I	Mixed mucous and pink staining eosinophilic cells
II	Mucous cells that stain with Alcian Blue
III	Basophilic cells that stain purple with Hemalum
IV	Neutrophilic cells that stain maroon in color
V	Metachromatic cells that stain dark blue
VI	Eosinophilic cells that stain pink with Eosin B

however, are longer than those lining the lumen. This channel is similar to that of *Nassarius reticulatus* (Linnaeus, 1758) described by FRETTER (1941). Since the staining regions of the capsule gland are complex, they are listed in Table 2 and their distribution is illustrated in Figure 3. The posterior region of the gland is largely composed of mucous cells and protein secreting cells, while the remainder consists of a complicated interrelationship of protein, mucus, and mucoprotein secreting cells. Figure 4 is a view of the capsule gland dissected along the mid-dorsal line exposing the ciliary tracts. It can be seen that the gland is subdivided into three functional regions based upon the predominant direction of the currents. Posteriorly in region A, the cilia beat in a cyclic manner, while in regions B and C the currents are directed obliquely towards and away from the ventral channel. The distribution of the

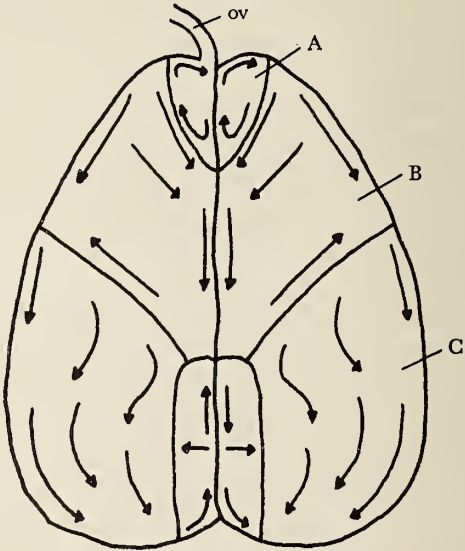
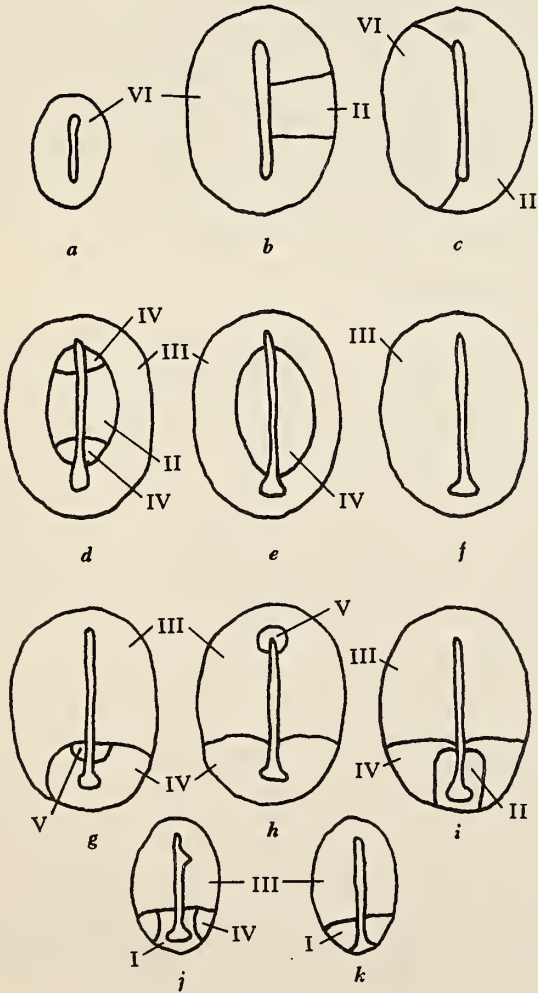


Figure 4

Ciliary Currents in the Capsule Gland of *Columbella fuscata*:  
A, B, and C - ciliary regions      ov - oviduct

(← adjacent column)

Figure 3

Sections through Various Regions of the Capsule Gland in *Columbella fuscata* showing the differential staining patterns: a through k - sections from posterior to anterior end of gland; I - mixed mucous and eosinophilic cells      II - mucous cells  
III - basophilic cells      IV - neutrophilic cells      V - meta-  
chromic cells      VI - eosinophilic cells



Table 3

Relationship of Ciliary Tracts to Staining Regions in the Capsule Gland of *Columbella fuscata*

Region	Thickness (micra)	Staining Pattern <sup>2</sup>	Cell Type	Secretion
A	400	a, b, c	II, VI	mucous and protein
B	1950	d, e	II, III, IV	mucous and muco-proteins
C	2100	f, g, h, i, j, k	I, II, III, IV, V	muco-proteins

<sup>2</sup>From Figure 3.

staining areas in relation to the ciliary tracts is shown in Table 3.

Posteriorly, the ventral channel gives rise to two openings. The posterior opening leads to the oviduct, while the anterior one opens into the convoluted gonopericardial duct (gop). This latter is quite large and can be easily removed from the living animal. When extended it reaches a length of 3 mm and measures about 70  $\mu$ m across. It is surrounded by a thin layer of circular muscle cells and lined with cuboidal ciliated epithelium, the cilia of which beat towards the pericardial cavity (pc). The opening into the cavity is guarded by a thick sphincter. The pericardial wall is ciliated on the left side and glandular on the right. The pericardial cavity is the site for sperm ingestion, which is discussed below.

The lumen of the capsule gland can be traced anteriorly where it empties into the deeply folded vestibule (ve). It is large and bulges into the mantle cavity when occupied by newly formed egg capsules. There is no musculature and the entire structure is surrounded by a thin layer of connective tissue. A short ciliated vagina connects the vestibule with the external genital opening. Histologically the vagina and vestibule are similar. In spawning females, a ciliated groove can be traced from the genital opening down to the region of the ventral pedal gland in the foot.

### Reproductive Systems of Additional Species

The gross anatomies of the species discussed below are illustrated in Figures 5, 6.

#### MURICIDAE

In males the vas deferens can either be convoluted as in *Thais emarginata*, *T. canaliculata*, *T. haemastoma*, *Trophon barvicensis*, *Urosalpinx cinerea*, and *Ocenebra japonica*; or more or less straight as in *Drupa nodulosa*,

*Trophon truncatus*, *Acanthina spirata*, and *Ceratostoma foliatum*. The upper end of the convoluted vas deferens acts as a seminal vesicle. Openings from the vas deferens into the mantle cavity in *Trophon truncatus*, *Acanthina spirata*, and *Ceratostoma foliatum* occur by means of a small ciliated duct located just posterior to the prostate gland. In these species there is also a sphincter located anterior to the seminal vesicle.

The prostate glands are typical of those described by FRETTER (1941) for *Ocenebra erinacea*. In *Thais canaliculata* and *Trophon barvicensis* the posterior region is not fused, and there is communication to the mantle cavity by a ventral slit.

No functional gonopericardial duct occurs in the males examined. There is, however, a remnant of a duct in *Acanthina spirata*. Histologically it appears as a thin strand of connective tissue (ct) joining the pericardial wall to the vas deferens.

All of the species have a penis which is flattened dorso-ventrally. The penial ducts are either centrally located or off to one side as in *Thais emarginata*, *T. canaliculata*, and *T. haemastoma*. This agrees with the findings of FRETTER (1941) for *Nucella lapillus* and *Ocenebra erinacea*. However, in *O. japonica* the penial duct is centrally located. In *Trophon truncatus* and *Trophon barvicensis* the penial duct is highly convoluted, and the anterior vas deferens runs for only a short distance before joining the prostate gland. This duct is much longer in the other species.

In females the vagina is a generally ciliated, muscular, and sometimes glandular tube running parallel to the rectum. This organ is, however, reduced to a small cavity in *Thais emarginata*, *T. canaliculata*, *T. haemastoma*, and *Drupa nodulosa*. This condition is also found in *Nucella lapillus* (FRETTER, 1941). The morphology of the bursa copulatrix is highly variable, and its location varies depending upon the species. It has the appearance of a bulbous sac just anterior and ventral to the capsule gland in *Thais emarginata*, *Acanthina spirata* and *Urosalpinx cine-*

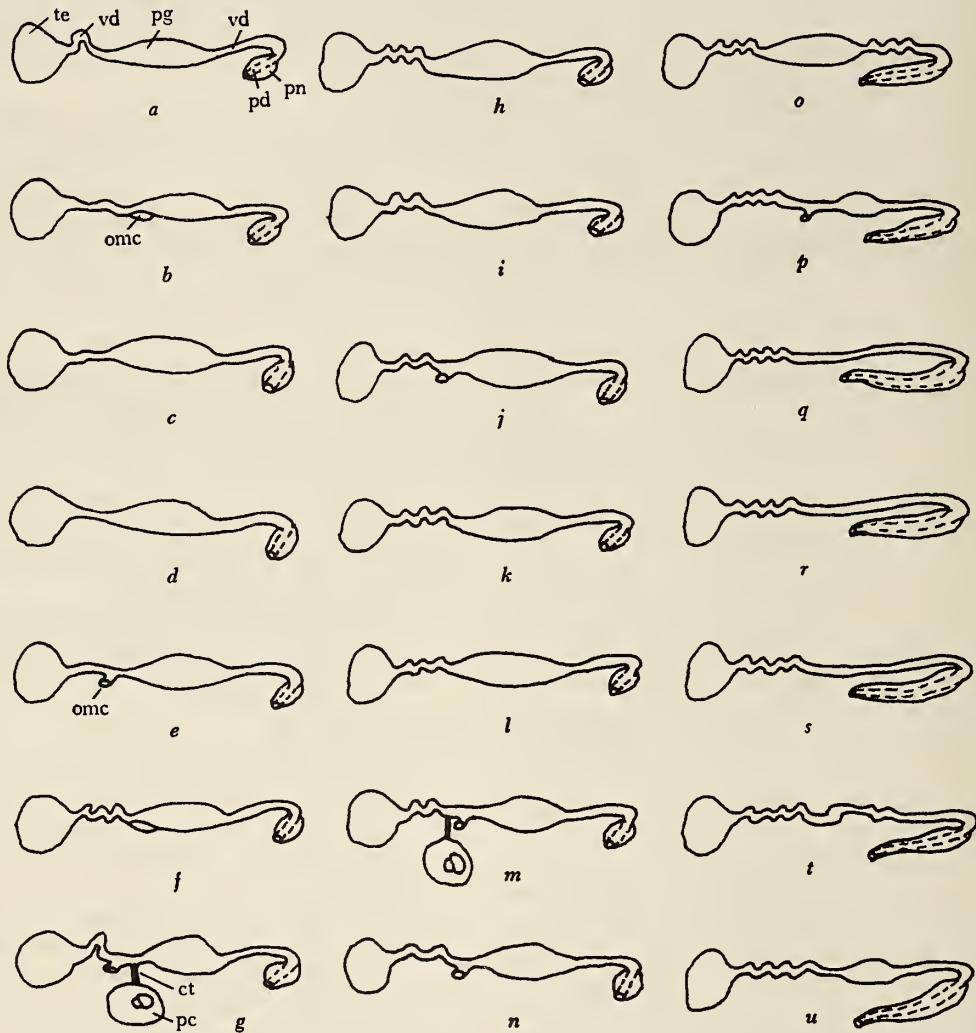


Figure 5

## The Male Ducts

*a* - *Thais emarginata*      *b* - *Thais canaliculata*      *c* - *Thais haemastoma*  
*d* - *Drupa nodulosa*      *e* - *Trophon truncatus*  
*f* - *Trophon barvicensis*      *g* - *Acanthina spirata*      *h* - *Ocenebra japonica*  
*i* - *Urosalpinx cinerea*      *j* - *Ceratomyxoma foliatum*  
*k* - *Colus gracilis*      *l* - *Neptunea anti-gua*  
*m* - *Cantharus dorbignyi*      *n* - *Pisania janierensis*  
*te* - testis

*o* - *Nassarius incrassatus*      *p* - *Mitrella guttata*      *q* - *Columbella strombiformes*  
*r* - *Anachis coronata*      *s* - *Anachis nigrofusca*      *t* - *Anachis sanfelipensis*      *u* - *Anachis varia*  
*ct* - connective tissue      *omc* - opening to the mantle cavity  
*pc* - pericardial cavity      *pd* - penial duct  
*pg* - prostate gland      *pn* - penis      *sv* - seminal vesicle  
*vd* - vas deferens

*rea*, as opposed to being dorsally located in *Thais canaliculata* and *Drupa nodulosa*. In *T. emarginata*, sperm can be seen attached to the bursal wall. The bursa is quite large

in *T. haemastoma*, while that of *Trophon barvicensis* is reduced to a small vesicle just posterior to the vagina.

The capsule glands are remarkably similar among the

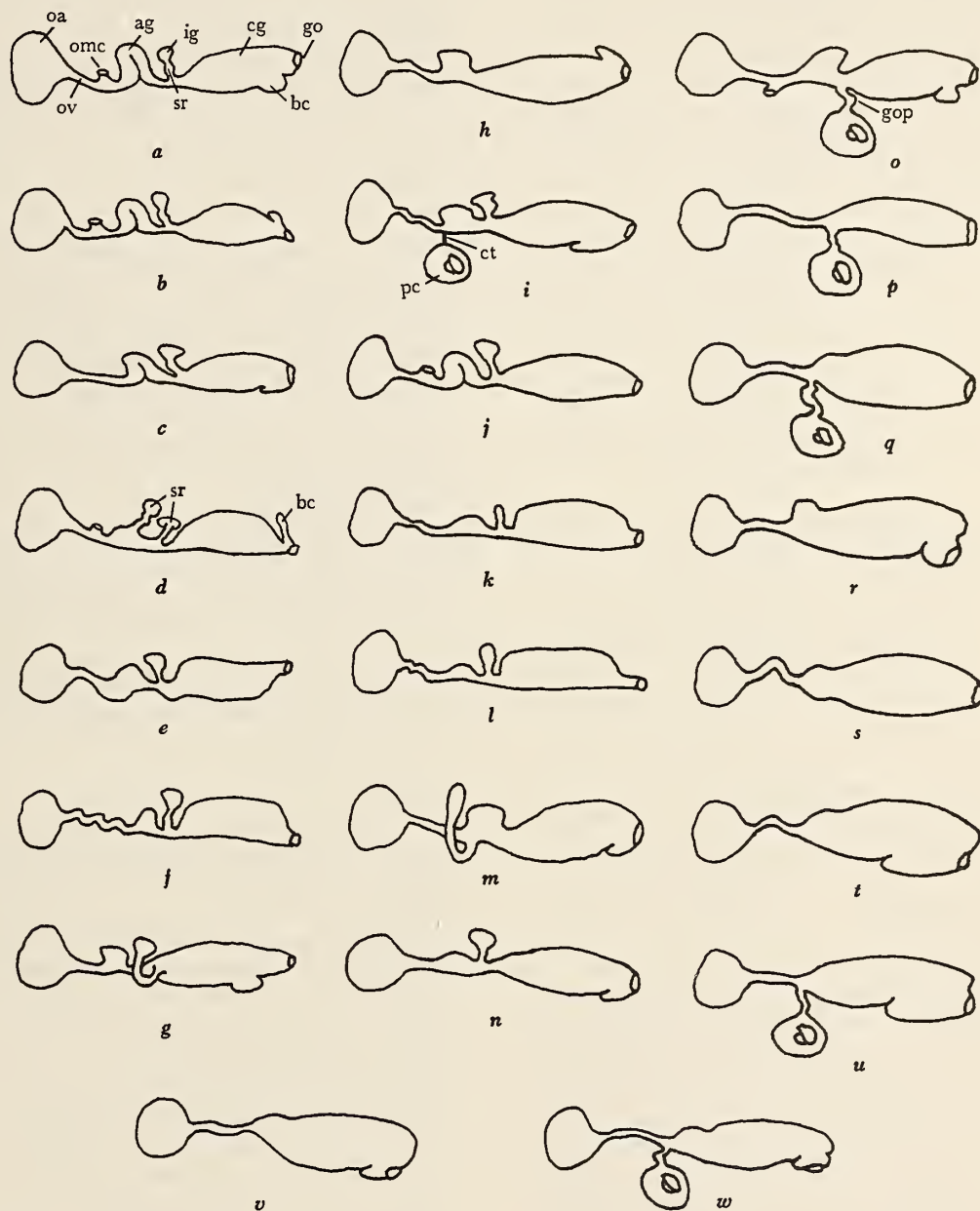


Figure 6

## The Female Ducts

*a* - *Thais emarginata*    *b* - *Thais canaliculata*    *c* - *Thais haemastoma*  
*d* - *Drupa nodulosa*    *e* - *Trophon truncatus*  
*f* - *Trophon barvicensis*    *g* - *Acanthina spirata*    *h* - *Ocenebra japonica*  
*i* - *Urosalpinx cinerea*    *j* - *Ceratomyxoma foliatum*  
*k* - *Colus gracilis*    *l* - *Neptunea antiqua*  
*m* - *Cantharus dorbignyi*    *n* - *Pisania janierensis*  
*o* - *Nassarius incrassatus*    *p* - *Mitrella guttata*    *q* - *Columbella strombiformes*  
*r* - *Parametaria duponti*    *s* - *An-*

*achis coronata*    *t* - *Anachis hilli*    *u* - *Anachis nigrofusca*  
*v* - *Anachis sanfelipensis*    *w* - *Anachis varia*  
ag - albumin gland    bc - bursa copulatrix    cg - capsule gland  
ct - connective tissue    gop - gonopericardial duct  
go - genital opening    ig - ingesting gland  
oa - ovary    omc - opening to the mantle cavity    ov - oviduct  
pc - pericardial cavity    sr - seminal receptacle



several species with the lumen appearing as a ciliated dorsoventral slit. The ventral channel in *Acanthina spirata* is almost a closed duct. There is no connecting duct, but only a slight constriction separating the albumin and capsule glands in *Ocenebra japonica* and *Urosalpinx cinerea*. In contrast, a duct joins the two glands in the other species. In *Thais emarginata*, *T. canaliculata*, *T. haemastoma*, and *Ceratostoma foliatum*, the albumin gland is doubled back on itself like a hairpin.

*Thais emarginata*, *T. canaliculata*, *T. haemastoma*, *Urosalpinx cinerea*, *Drupa nodulosa*, *Acanthina spirata*, and *Ceratostoma foliatum* have an ingesting gland. The ducts to these glands originate from the posterior region of the capsule gland. The lumina of the glands are composed of numerous blind diverticula containing masses of sperm. Sperm ingestion was observed in *Thais emarginata*, *T. canaliculata* and *U. cinerea*. *Ocenebra japonica*, *Trophon truncatus* and *T. barvicensis* do not have an ingesting gland.

The duct to the ingesting gland in *Thais canaliculata* is modified as a seminal receptacle. Although no sperm ingestion was observed in *Trophon truncatus* and *Trophon barvicensis*, similar ducts arise from the posterior region of the capsule gland which end in glandular vesicles. In *Tr. barvicensis* sperm heads can be seen attached to the epithelial walls of the vesicle. Hence, these regions serve as areas for sperm storage. The seminal receptacle in *Drupa nodulosa* and *Thais haemastoma* is separate and lies posterior to the ingesting gland. It consists of a convoluted duct ending in a small bulb that is embedded within the nephridium. The ventral channels in *Th. emarginata* and *Urosalpinx cinerea* give rise to elongated sacs for sperm storage. In *T. emarginata* the sac lies to the left of the ventral channel, and in *U. cinerea* it lies to the right. It can be seen as a bulging ridge along the right side of the capsule gland in the living animal. In both species this sac is open to the ventral channel throughout its entire length, until it reaches the posterior region of the gland. In this area it fuses into a duct that crosses over to the opposite side and opens into the ingesting gland. Spermatozoa within these sacs are neatly arranged with their heads attached to the epithelium, and their tails extending into the lumen. No seminal receptacles have been observed in *Ocenebra japonica*, *Ceratostoma foliatum*, and *Acanthina spirata*.

Both *Thais haemastoma* and *Drupa nodulosa* have a gonopericardial duct, which connects the pericardial cavity with the pallial oviduct, just anterior to the albumin gland. The ducts are ciliated and are guarded by a sphincter upon entering the cavity. In *Ocenebra erinacea* the duct opens into the cavity through a prominent ciliated funnel instead

of a sphincter (FRETTER, 1941). The duct has disappeared in *Urosalpinx cinerea* and is represented by only a thin strand of connective tissue.

The posterior region of the oviduct in *Thais emarginata*, *Th. canaliculata*, *Drupa nodulosa*, and *Ceratostoma foliatum* is open to the mantle cavity via a short ciliated duct.

#### BUCCINIDAE

The gross morphology of the male genital tracts of buccinids in this study is similar to that of *Buccinum undatum* described by FRETTER (1941). The upper end of the vas deferens is coiled and serves as a seminal vesicle. In *Cantharus dorbignyi* a sphincter muscle is present just anterior to the seminal vesicle. The presence of connective tissue joining the pericardial wall to the vas deferens indicates a remnant of a gonopericardial duct in this species. Also, the vas deferens is open to the mantle cavity via a short ciliated duct.

The major difference in the gross morphology of female genital tracts of buccinids, as compared to those of muricids, is the location of the duct to the ingesting gland. In *Cantharus dorbignyi* this duct originates from the albumin gland, as opposed to the capsule gland in muricids. *Nepitunea antiqua*, *Colus gracilis*, and *Pisania janiensis* have no ingesting gland. The seminal receptacle in *N. antiqua* and *C. gracilis* is divided with one sac on each side of the ventral channel.

#### NASSARIIDAE

The reproductive system of *Nassarius incrassatus* is quite different from that of *N. reticulatus* described by FRETTER (1941).

The vas deferens of the male is greatly coiled at the upper end like that of the buccinids. The prostate gland is interesting in that it is surrounded by a thick muscle layer and becomes convoluted at its anterior end. Leaving the prostate is the coiled, muscular, anterior vas deferens that terminates in a tubular penis.

In the female the muscular vagina leads into the bursa copulatrix, which appears as a pouch located ventral to the capsule gland. According to JOHANSSON (1957), a seminal receptacle and ingesting gland exist in this species. However, both organs are absent in the specimens examined for this study. There is a ciliated gonopericardial duct that joins the ventral channel near the posterior region of the capsule gland. Within this gland was a partially formed egg capsule containing numerous eggs. A sphincter muscle controls the posterior entrance to the large albumin gland. A short duct from the oviduct opens into the mantle cavity about halfway between the albumin gland and the ovary.

## COLUMBELLIDAE

Unfortunately no male specimens of *Anachis hilli* and *Parametaria duponti* were collected. Therefore, their genitalia were not studied.

The upper vas deferens in all male columbellids in this study is modified into a seminal vesicle. It is interesting to note that one specimen of *Anachis varia* had a vas deferens which bifurcated and rejoined, resulting in a double duct. In *Mitrella guttata* a sphincter muscle is present just anterior to the seminal vesicle.

A prostate gland is present in *Mitrella guttata*, *Anachis varia*, and *A. sanfelipensis*. It appears as an elongated glandular mass in *M. guttata* and *A. varia*, as opposed to a coiled duct in *A. sanfelipensis*. The anterior vas deferens is highly muscular and weakly ciliated in all of the species examined. The penes are similar to that of *Columbella fuscata* in that they are wide at the base and taper to a pointed tip. In addition, all of these species have a pouch in the posterior mantle roof into which the penis is tucked when not in use.

An opening from the vas deferens into the posterior mantle cavity is present only in *Mitrella guttata*. This opening differs from that of *Columbella fuscata*, in that it appears as a short ciliated duct arising from the posterior vas deferens.

The female systems of these species are basically similar to that of *Columbella fuscata*, except for the following features. *Anachis sanfelipensis* has a large muscular bursa copulatrix which is non-ciliated. This structure acts as a seminal vesicle because females that had previously copulated were found to contain sperm neatly arranged in rows. Sperm storage also occurs in the bursae of *Anachis brasiliana*, *A. sparsa*, and *A. veleda* (MARCUS & MARCUS, 1962b). *Anachis coronata*, *A. varia*, and *Parametaria duponti* have an albumin gland which occupies the posterior tip of the capsule gland. *Columbella fuscata* has no albumin gland. A gonopericardial duct is present in *A. varia*, *A. nigrofusca*, *C. strombiformes*, and *M. guttata*.

As in *Columbella fuscata*, sperm ingestion occurs in the pericardial cavity of *Mitrella guttata*. Here the sperm are shunted to a diverticulum off the main cavity, where they are broken down by the epithelial cells.

## Egg Capsules

*Columbella fuscata*

In this species, spawning occurs throughout the year with peak periods from June through August, and November through the middle of February. Females deposit their capsules on the seaweeds *Padina* and *Sargassum*. Individ-

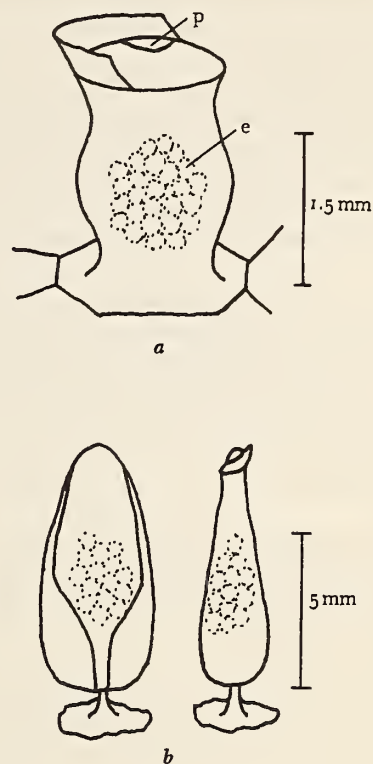


Figure 7

Egg Capsules  
a - *Columbella fuscata*      b - *Acanthina angelica*  
e - eggs      p - mucous plug

ual females can deposit up to 40 capsules; however, the average mass contains about 20. The light brown capsules are deposited in alternating rows and average 2.2 mm in height and 1.5 mm in width. They are flask shaped and are attached to the algae by an adhesion disk, (Figure 7a). The top is surrounded by a flanged collar, and the mucous plug is centrally located.

There are about 50 eggs (e) in each capsule which are distributed in a loosely packed mass. There is no apparent albumin present around the eggs.

The histology of the capsule wall is shown in Figure 8a. The wall of the capsule is made up of 4 layers. The thin innermost mucous layer is homogeneous and transparent. The two middle layers consist of oblique protein fibers directed in a crisscross network. The outer layer, which is secreted by the ventral pedal gland, is composed of mu-



cus. The formation of the egg capsule is discussed below.

#### *Acanthina angelica*

The egg capsules of this species were briefly described earlier by WOLFSON (1970). *Acanthina angelica* spawns from the middle of December through the last week in March. Females aggregate in large numbers underneath the basaltic boulders to deposit their capsules. These egg masses can be quite large, sometimes numbering up to 500 capsules.

The bright yellow capsule averages 5 mm in height and 2 mm in width. It is vase-shaped and attached to the substratum by a short stalk (Figure 7b). The surface of one side is flat and bordered by two longitudinal ridges running the length of the capsule. The top is sealed by a round mucous plug which dissolves away when the juveniles hatch. The walls are translucent and the egg mass can be seen within.

The yellow eggs are rather large and yolky, reaching a diameter of about 250  $\mu\text{m}$ . In freshly laid capsules, the eggs are compacted into a mass of 400-500 in number and surrounded by a coat of albumin.

Histological sections reveal the three layers that compose the capsule wall (Figure 8b). The innermost layer is thin and homogeneous and stains with Alcian Blue. The middle and outer layers are fibrillar in appearance and

stain pink with Hemalum and Eosin B. In addition, a homogeneous substance is dispersed among the fibers. The direction of the fibers in the middle layer is circular, while that of those in the outer layer is longitudinal. In capsules from *Nucella lapillus*, FRETTER (1941) showed that the circular fibers make up the outer coat, while the middle layer is longitudinal. ANKEL (1973) proposed that the egg capsule of the same species is composed of two substances, the protein and conchiolin intermixed with mucus or a mucoid substance. This has been substantiated in histochemical studies by BAYNE (1968), in which acid mucopolysaccharides and conchiolin were found to be the major components of the capsule wall.

#### Reproduction in *Columbella fuscata*

##### Copulatory behavior

Copulation in *Columbella fuscata* occurs in the sand around the bases of *Padina* and *Sargassum*. When the mates pair, the male crawls onto the shell of the female and grasps the anterior siphonal canal with his epipodial palps. At this point, both male and female are lying side by side, with their anterior canals facing in the same direction. The penis is removed from the posterior pouch and inserted into the genital aperture of the female. When this occurs there is a slight twisting movement of both partners. Ejaculatory movements occur at 5 second intervals for about one minute. At this time, the male jerks violently while the female remains more or less motionless. Soon after ejaculation is completed, the male withdraws the penis while the female rises up on her foot and twists rapidly from side to side until the male falls off. The entire process takes up to 25 minutes. During this time, 10 to 15 minutes are spent in precopulatory attachment.

##### Egg string movement

Eggs are released, one at a time, from the ovary into the oviduct in females dissected prior to copulation. At this time, the oviduct is distended to one and one-half its original diameter. The eggs are surrounded by large amounts of yolk and situated toward the edge of the yolk mass. This orientation exposes a region of the egg membrane for sperm entry during fertilization. The yolk and eggs are transported in single file by cilia along the oviduct. As they enter the capsule gland, the ova can be seen disappearing one by one. The journey from the ovary to the capsule gland takes from 10 to 15 minutes.

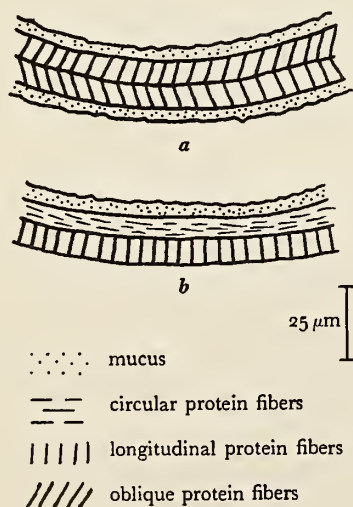


Figure 8

Egg Capsule Histology

a - *Columbella fuscata*

b - *Acanthina angelica*



### Sperm movement in the male

Spermatozoa are released from the seminal vesicle upon relaxation of the sphincter muscle. From this point, they are transported mainly by ciliary action along the posterior vas deferens. The ciliary tracts are arranged in spiral fashion, thereby drawing the sperm mass out into a helioid configuration (Figure 9). This probably aids in mixing the sperm evenly with prostatic secretions. When the sperm enters the anterior vas deferens, it is moved mostly by peristaltic contractions towards the penis. The sphincter near the entrance to the diverticulum closes, thus preventing any loss of seminal fluid. However, in snails that are dissected during copulation, sperm can be observed escaping into the mantle cavity through the opening in the

the vestibule, where the tip is directed downwards and inserted directly into the ventral channel. Two muscular strips posterior to the genital opening hold the penis in place. Males observed after copulation show a constriction near the anterior end of the penis, which is produced by these muscular strips. The region anterior to the constriction is about 1.5 mm in length, which is the same length as that of the vestibule. Sperm released in the ventral channel move, with the aid of cilia, to the posterior region of the capsule gland where fertilization takes place.

In females dissected soon after copulation, sperm not utilized in fertilization can be observed moving through the gonopericardial duct and filling the pericardial cavity (Figure 12). The cavity is about one-half full in females dissected 5 minutes after copulation, and completely full

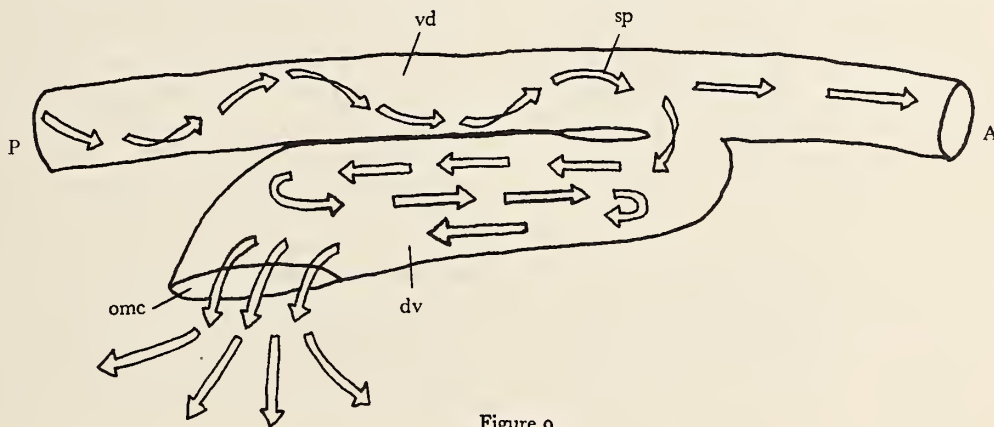


Figure 9

#### Sperm Movement in a Male *Columbella fuscata*:

dv - diverticulum      omc - opening into the mantle cavity  
sp - sperm      vd - vas deferens      A - anterior      B - posterior

diverticulum. The sphincter at the entrance to the diverticulum relaxes and the sperm is shunted into this region. Concurrently the sphincter at the anterior end of the seminal vesicle closes, thereby preventing any backward movement. As the sperm enters the diverticulum, it congregates into a large mass completely filling the region before it is extruded (Figure 9). Cilia in the diverticulum then direct the entire sperm mass through the opening and into the posterior mantle cavity. Small quantities of sperm are also extruded through the penial opening.

### Sperm movement in the female

During copulation the penis is inserted into the female aperture. The apical portion of the penis passes through

after 10 minutes. The normally transparent cavity now attains a white opaque appearance.

### Fertilization

Fertilization occurs in the lumen of the posterior region of the capsule gland. As the unfertilized eggs (ue) enter the capsule gland, they come into contact with spermatozoa from the ventral channel (Figure 10). Dissections of females during the first 10 minutes after copulation show the eggs being mixed with the sperm mass.

### Sperm ingestion

As the pericardial cavity becomes filled with sperm, cilia lining the left side of the pericardial wall drive the sperm



When the males are 12.1 mm long, the testis is undifferentiated with only a thin layer of connective tissue lin-

ing the upper end of the testicular duct. This thin-walled duct is fused throughout its entire length and filled with loosely packed strands of connective tissue. Anteriorly, the duct straightens out and passes along the right side of the visceral mass. As it approaches the region of the kidney, it opens up into seminal groove, which continues underneath the right mantle wall until it reaches the mantle fold. Here it curves left and passes along the right body wall to the base of the rudimentary penis. There is no evidence of a prostate gland or prostatic tissue at this stage of development. The penis appears as a bulge of pedal tissue, 200  $\mu$ m long, posterior to the right cephalic tentacle. The penial duct is fused for about 110  $\mu$ m, then reopens near the anterior end of the penis. A double row of columnar cells defines the line of fusion in the duct.

When the juveniles reach a length of 13.5 mm, the testis begins to differentiate. It consists of several layers of proliferating round cells that have large nuclei. A thin sheet of connective tissue separates the young testis from the digestive diverticula. The testicular duct still contains connective tissue. Anteriorly the vas deferens is now fused into a closed duct which opens into the rudimentary prostate region. This region is also fused throughout its length, except for the posterior area. No glandular tissue has developed yet, and the epithelium lining the lumen is composed of tall ciliated columnar cells. Anterior to the prostatic region, the pallial vas deferens is fused along its entire length and joins the base of the penis. The well differentiated penis is 1.5 mm long and contains a centralized penial duct, of which only the anterior region is a ciliated groove.

By the time juveniles attain a length of 15.0 mm, the testis is well developed with many acini and primordial germ cells. The testicular vas deferens is clear of connective tissue and the prostatic region is becoming glandular. The pallial vas deferens and penial duct are completely fused throughout their entire length. Only one juvenile female was collected and it measured 15.8 mm in length. The ovary was undeveloped and only a thin layer of connective tissue surrounded the upper end of the gonadal oviduct. This duct was lined with cuboidal epithelium and contained strands of loosely packed connective tissue. Anteriorly the oviduct was fused along its entire length. The pallial oviduct, however, was only a straight tube without accessory glands and structures, except for a small diverticulum about 16  $\mu$ m in length. The diverticulum originated dorsally just anterior to the kidney. It was non-ciliated and probably gives rise to the seminal receptacle and ingesting gland.

#### *Columbella fuscata*

The development of the male genital duct in this species is remarkably different from that of *Acanthina angelica*. In juveniles 10.0 mm and 11.0 mm in length, the penis is fairly well developed and about one millimeter long. The penial duct is fused but there is no line of fusion present. Posteriorly the closed pallial vas deferens passes along the right body wall, then disappears in the region of the mantle fold. It is lined with ciliated cuboidal epithelial cells and covered with a thin layer of connective tissue. The remainder of the genital duct, along with the testis, is not discernible. When the juveniles attain a length of 13.0 mm, the reproductive system is complete. The testis is not completely developed. However, it consists of many acini, and spermatogenesis is occurring with many spermatogonia and primary spermatocytes present. The seminal vesicle is highly convoluted but it is devoid of sperm. The penis and anterior vas deferens are extremely muscular and well developed. In addition, the diverticulum leading to the opening into the posterior mantle cavity is present.

In females the development is again from the anterior to the posterior. Juveniles which are 16.5 mm long have a genital opening that leads to a well developed ciliated vestibule. This opens into a slightly smaller duct, which is lined with ciliated columnar epithelium and surrounded by a thin layer of connective tissue. This region will apparently become the capsule gland; however, at this time there is no glandular tissue present. Posteriorly the duct bifurcates with the dorsal branch giving way to the oviduct, while the ventral branch is a diverticulum projecting towards the pericardial cavity. The oviduct continues posteriorly for a short distance, then disappears as a diffuse mass of connective tissue. Moreover, the ovary is not apparent at this time.

When females reach a length of 18.0 mm, the diverticulum has joined the pericardial cavity, forming the gonopericardial duct. In addition, the pallial oviduct is enlarged but there is still no indication of any glandular tissue.

## DISCUSSION

The general plan of the genital systems in the species studied is relatively uniform; however, both anatomical and functional differences occur within the accessory structures. Of particular interest are the occurrence of mantle openings in the male, and sperm receiving and storage organs, and gonopericardial connectives in the female.



### Evolution of the Open Reproductive System

A hypothesis for the evolution of mantle (pallial) gonoducts was proposed by JOHANSSON (1942), and FRETTER (1946). They suggested that the gonoducts in both sexes were originally open, ciliated grooves, bordered by glandular tissue. This condition is quite evident among the mesogastropods. Studies by JOHANSSON (1946) of *Turritella communis* Risso, 1826, *Bittium reticulatum* (da Costa, 1778) (JOHANSSON, 1947) and *Cerithiopsis tubercularis* (Montagu, 1803) (FRETTER, 1951) revealed the fact that open ducts occur in both sexes. In addition, JOHANSSON (1953) examined *Cerithium vulgatum* Bruguière but unfortunately was able to collect only male specimens, all of which, nevertheless, had open seminal grooves.

At this place it is appropriate to mention that several species of mitriform neogastropods retain the primitive open condition. WOODWARD (1901) wrote that the entire pallial duct of *Adelomelon ancilla* [Lightfoot, 1786] is a long groove. In a study of *Alcithoe arabica* (Gmelin, 1791) PONDER (1970) notes that the prostate is completely open along the ventral surface. Also, in a later report, PONDER (1972) observed a seminal groove in *Peculator hedleyi* (Murdoch, 1905).

As the mesogastropods and neogastropods evolved, the pallial groove became fused into a duct along its entire length (FRETTER, 1946). KRULL (1935) found this to be true for the hybriid, *Assimineia grayana* Fleming, 1828. According to PONDER (1973), closure of the prostate gland arose independently in several families. In *Triva monacha* (da Costa, 1778) and *T. arctica* (Montagu, 1803) (FRETTER, 1946) and *Circulus striatus* (Philippi, 1836) (FRETTER, 1956), the posterior region of the prostate gland is open to the mantle cavity by a ventral slit. As mentioned earlier, similar openings occur in many of the British *Stenoglossa* (FRETTER, 1941), columbellids (MARCUS & MARCUS, 1962b), olivids (MARCUS & MARCUS, 1959a), and turrids (SMITH, 1967). Moreover, this condition occurs in most of the species in this study (Figures 1, 5). It is interesting to note that the opening occurs in several different ways. In *Thais canaliculata* and *Acanthina angelica* it appears as a ventral slit in the posterior region of the prostate. In contrast, it is a short ciliated duct in *Cantharus dorbignyi* and *Acanthina spirata*. In *Columbella fuscata* the opening is unique in that it occurs on the surface of a diverticulum ventral to the vas deferens.

In accordance with the open groove theory, it would appear that these openings are a retention of the primitive condition and therefore are of primary derivation. The ontogenetic studies of *Columbella fuscata* and *Acanthina angelica* give support to this hypothesis. Posterior open-

ings are present even in the youngest of juveniles, which would indicate they are primary. This condition probably exists in other species, but has yet to be determined.

The pallial opening is doubtfully pleiotropic because of its widespread occurrence in different genera. FRETTER (1941) suggests that it acts as a "safety valve" in providing an escape for sperm when males are disturbed during copulation. The author agrees with her hypothesis because this was observed repeatedly in *Columbella fuscata*. Also, there is a close relationship between the pallial opening and the presence of a sphincter muscle anterior to the seminal vesicle. Species that have a mantle opening also have the sphincter. Further, the seminal vesicle is thin and fragile. Conversely, the opening and sphincter muscle are absent in those species that have an elastic seminal vesicle. Therefore it is apparent that if the opening was not present, pressure resulting from seminal fluid would rupture the vas deferens, because the sphincter contracts and prevents any backward movement of seminal fluid. In those species without the opening, the seminal vesicle can expand and absorb the excess pressure. It is important to have some protective mechanism. Because the copulatory period in gastropods can be rather long, a protective mechanism of this sort has high survival values. MARCUS & MARCUS (1959b) observed that copulation lasts up to 3 hours for *Olivella verreauxii* (Duclos, 1857). During this time, vulnerability to predation and physical parameters, such as waveshock, is increased.

The length and shape of the prostate gland are quite variable. The gland is especially long in turrids (SMITH, 1967), probably owing to the narrowness of the mantle cavity. It is well known that the prostate gland provides a liquid medium for the spermatozoa, for transference from male to female. This gland, however, is absent in several species of columbellids. Instead, the seminal vesicle is glandular and appears to assume a prostatic function in addition to sperm storage and resorption.

The penes can be separated into two morphological types. Those that are wide, blunt, and considerably flattened dorsoventrally, and those that are wide, tapering to a point, and flattened or tubular. The first type occurs in the muricids and buccinids, whereas the second type occurs in nassariids, columbellids, olivids, and turrids. Studies by PONDER (1972) on mitriform gastropods indicate they have penes similar to those of the olivids. The penis, in addition to functioning as an intromittent organ, also aids in holding the copulating partners together. In *Littorina irrorata* (Say, 1822), BINGHAM (1972) observed that the penis is directed into the mantle cavity of the female, where it quickly inflates. It is possible that penes which are wide and blunt never actually enter the female aperture, but

only the mantle cavity, where they release their gametes. Respiratory currents would then carry the gametes to the female opening. This has been suggested for *Buccinum undatum* (Linnaeus, 1758), because the gigantic penis could in no way be inserted into the minute distal bursa copulatrix of the female (JOHANSSON, 1953). Also, ciliary currents are directed towards the bursa. This appears to be the case for *Acanthina angelica*, other muricids, and buccinids. On the other hand, in *Columbella fuscata* the penis does enter the female aperture and is held in place by muscular strips bordering the vestibule. This most likely occurs in other columbellids and other groups with this type of penis. An exception is *Olivella verreauxii*, which has a long narrow penis that is inserted only into the mantle cavity of the female. Here the sperm are transported by cilia to a groove leading to the oviducal opening (MARCUS & MARCUS, 1959b). The mucous glands in the penis may assist in the insertion and securement in the female. FRETTER & GRAHAM (1962) believe this to be true for *Littorina irrorata*.

JOHANSSON (1953) suggests that when the oviducal groove in females was transformed into a closed duct, a posterior or proximal opening would have been necessary for those forms lacking a penis because sperm transport and reception were dependent on ciliary currents. In the Neritidae and Helicinidae, BOURNE (1911) remarks that the vagina resulted from incomplete fusion of the oviducal groove, and is homologous with the posterior mantle opening in males. This condition is also present in *Nerita birmanica* (Phillipi, 1844), (BERRY, LIM & KUMAR, 1973), where the vagina is separate from the nidimental opening.

A proximal opening, however, occurs in some species that have a penis. Both the females of *Skeneopsis planorbis* (Fabricius, 1780) and *Rissoella diaphana* (Alder, 1848) have a proximal opening, and the males have a penis (FRETTER, 1948). JOHANSSON (1947) tried to associate the open oviduct with the absence of a penis. He found, however, that *Melania crenulata* (Swainson) and *M. tuberculata* (Müller) have no penis and the females have a closed oviduct. Conversely, in a later study JOHANSSON (1953) showed that *Melania intermedia* (Cantraine, 1835) has a penis and the female has a closed oviduct. As shown in Figure 6 females of *Thais emarginata*, *T. canaliculata*, *Cerastoma foliatum*, and *Drupa nodulosa* also have posterior openings in their oviducts. FRETTER (1951) believed that the open condition is secondary and tried to correlate it with the shape of the shell and the narrow mantle cavity. This is applicable for such genera as *Bittium*, *Cerithiopsis*, and *Triphora*. However, in *Trivia* and *Littorina*, which also have the open condition, the shell is quite different

and the mantle cavity is spacious. Fretter realized this and proposed that the alteration in shell shape may be recent and that the anatomy of the reproductive system has not had enough time to change from its ancestral condition. The author suggests that an external shell is more subject to environmental changes than internal systems. However, JOHANSSON (1953) remarks that a retention of a primarily open condition may also be due to the initial shape of the shell. Either hypothesis could be clarified by studies of the fossil record and ontogeny of these species.

The higher Prosobranchs have evolved a distal bursa copulatrix to receive the sperm during copulation. This is a definite advantage, especially in those species with a narrow mantle cavity. If the opening was posteriorly located, it would be difficult to accommodate a large penis (FRETTER, 1953). This would interfere with respiratory currents and other vital functions of the mantle cavity. As mentioned earlier, the bursa in the muricids and buccinids is much too small to receive the penis. Therefore, the sperm are released in the mantle cavity and carried to the bursa by ciliary currents. In the higher neogastropods this structure is compatible and functions as a penial receiving organ. Studies by MARCUS & MARCUS (1959a) reveal an extremely long muscular bursa in females of *Oliva sayana* (Ravenel, 1834). This would indicate it functions in holding the penis securely during copulation.

The bursa copulatrix, as a penial receiving organ, has evolved throughout the hermaphroditic gastropods. In the Opisthobranchiata the mantle cavity is reduced or absent, and in copulating partners the penes are inserted directly into the vaginal openings (EALS, 1921; PELSENER, 1935). Moreover, in the Pulmonata, the genital duct has separated from the mantle and now lies within the haemocoel. Here again, the penis is inserted directly into the vagina. In *Ariolimax californicus* (Cooper, 1872), the vagina is surrounded by a huge intrinsic muscle which firmly grasps the penis (MEAD, 1943). It is interesting to note that sometimes partners will apophallate to effect separation. To date, this phenomenon has not been observed in the Prosobranchs.

Seminal receptacles occur throughout the mesogastropods and have probably evolved in connection with the posterior copulatory opening (JOHANSSON, 1942). This condition is retained in many neogastropods, in which it is located posteriorly between the albumin and capsule glands. In these, the sperm received by the female is transported posteriorly along the ventral channel to the seminal receptacle, where it is stored. In *Thais emarginata* and *Urosalpinx cinerea* the ventral channel is modified into an anterior sperm sac. This structure reveals a clear homol-



ogy between the ventral channel and the seminal receptacle. Observations by MARCUS & MARCUS (1962b) indicate that in some species of columbellids the bursa copulatrix is divided into two sacs. One sac serves as a site for sperm ingestion, which is discussed below, while the other is used for sperm storage. A similar case is known from the Rissoidae (JOHANSSON, 1957). It appears, at least in some species, that a homology exists between the seminal receptacle and the bursa copulatrix.

FRETTER (1941) has observed in *Nucella lapillus* that the seminal receptacle opens into a diverticulated sac, which functions as an ingesting gland. This also occurs in *Acanthina angelica*, *Thais emarginata*, *Urosalpinx cinerea*, and several other neogastropods. FRETTER (1941) suggests that the ingesting gland is homologous with the seminal receptacle of other species. The diverticulum which arises from the oviduct in juvenile *Acanthina angelica* was found in the present study to be the common root for both the seminal receptacle and ingesting gland. This evidence clearly supports Fretter's view that a homology exists.

The gonopericardial duct, which occurs in several of the species studied, warrants some discussion. MARCUS & MARCUS (1962b) indicate that it is homologous to the right ureter of Archaeogastropods. The author disagrees with this hypothesis because the ontogeny of the gonopericardial duct in *Columbella fuscata* reveals a double origin. Both the pallial oviduct and the pericardial wall produce diverticula that eventually join in forming the canal. A similar condition occurs in *Littorina saxatilis* (Olivi, 1792) (COUSIN, 1972). MARCUS & MARCUS (*op. cit.*) have observed sperm storage in this duct and conclude that it functions as a seminal receptacle. It therefore appears that the gonopericardial duct is indeed homologous with the seminal receptacle of other species. Although this duct is usually confined to females, SMITH (1967) found that one exists in the male of *Lora trevelliiana* (Turton, 1834). Moreover, in *Acanthina spirata* a dense strand of connective tissue connects the vas deferens with the pericardial cavity, which suggests that it is the remnant of a duct.

As far as the capsule and albumin glands are concerned, it is apparent that homologies exist among those species with closed oviducts and those with open oviducts. JOHANSSON (1957) remarks that there is a definite homology between the albumin gland of neogastropods and the uppermost gland of *Littorina saxatilis* and *Alvania reticulata* (Carpenter, 1866). He also indicates that the ventral channel of neogastropods is equivalent to the vaginal lumen of the Rissoacea.

The ventral channel is interesting because, as previously mentioned, in *Thais emarginata* and *Urosalpinx cinerea*

it is modified into a seminal receptacle. Also, in *Acanthina angelica* and other muricids, its roof is composed of two longitudinal flaps of tissue which make it a functionally separate duct. This may indicate a homology to the functionally separate spermooviducts in hermaphroditic gastropods. If this were true, it would support the hypotheses of DUNCAN (1960) and GHISELIN (1965) in that the separation of the spermiduct and oviduct in the pallial region represents an advanced condition. Furthermore, this would disagree with SOLEM (1972) in that the monaulic pallial spermooviduct is the advanced situation. This, however, is speculation and much work is needed in this area. In addition, the hermaphroditic turrid, *Lora turricula* (Montagu, 1803), described by SMITH (1967) has morphologically separate male and female systems.

Several hypotheses are presented to account for sperm ingestion in gastropods. In *Eupleura caudata* (Say, 1822) and *Urosalpinx cinerea*, HARGIS & MACKENZIE (1961) argue that if sperm left over from one mating is not completely ingested, then it is viable for the next spawning period. They also suggest that sperm ingestion would be a way of disposing of "sick sperm," which would otherwise penetrate ripe ova and block the passage of viable sperm. In a recent study on *Helix pomatia* Linnaeus, 1758, LIND (1973) suggests that sperm ingestion is a way of possibly preventing self-fertilization. This, however, would not apply to neogastropods because they are generally not hermaphroditic. The author agrees with the suggestion of FRETTER (1941) that ingested sperm serve as nourishment for the adult. In reproductively active females the digestive gland is highly reduced; therefore, it would be advantageous to utilize excess sperm for nourishment. Also, in *Columbella fuscata*, occasionally ova and yolk granules are ingested by the pericardial epithelium.

### Egg Capsules

The egg capsules of *Acanthina angelica* are typically stenoglossan. This is also the case for *Thais emarginata*, *Thais canaliculata* (HOUSTON, 1971) and *Torvumurex territus* (Reeve, 1845) (MURRAY, 1964). On the other hand, the oyster drill *Bedeva hanleyi* (Angas, 1867) deposits lens-shaped capsules (HEDLEY, 1916). The egg capsules of *Columbella fuscata* are similar to those of the columbellid *Anachis brasiliiana* described by MARCUS & MARCUS (1962b). FRETTER & GRAHAM (1962) state that in neogastropods the shape of the cavity of the ventral pedal gland resembles that of the egg capsule. In these species it was extremely difficult to detect any relationship.